MycoKeys

MycoKeys 129: 1–22 (2026)
DOI: 10.3897/mycokeys.129.179449

Research Article

Two novel species belonging to *Psathyrella* sections *Atomatae* and *Hydrophilae* (Psathyrellaceae, Agaricales) from Yunnan Province, China, based on morphological and multi-locus phylogenetic analyses

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Abstract

This study describes two collections of saprobic gilled mushrooms morphologically identified as *Psathyrella* and collected in Qujing, Yunnan Province, China. Based on multi-gene phylogenetic analyses of nrITS, nrLSU, and *tef*-1α sequences, two collections were confirmed to belong to the *Psathyrella* sections *Atomatae* and *Hydrophilae*. Morphologically, *Psathyrella qujinguniversitatica* (*Psathyrella* sect. *Atomatae*) is characterized by small basidiomata, a beige to light brown pileus, large basidiospores, and partially thick-walled cheilocystidia, while *P. yunnanensis* (*Psathyrella* sect. *Hydrophilae*) is characterized by a pileus that gradually changes from orange-brown to lighter towards the margin, with the edge light brown to brown, distinct striations, a fibrillose veil, larger basidia, and partially thick-walled cheilocystidia. Descriptions, illustrations, and phylogenetic analyses of the two new species are provided. In addition, the present study updates the number of *Psathyrella* species reported from China to 55, along with their known distribution.

Key words: Morphology, new species, phylogeny, psathyrelloid fungi, taxonomy

OPEN ACCESS

Academic editor: Entaj Tarafder
Received: 23 November 2025
Accepted: 26 January 2026
Published: 19 February 2026

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Citation: Zheng D, Tibpromma S, Lu W, Han M, Suwannarach N, Elgorban AM, Alfagham AT, Yu F, Dai D, Zhang L, Karunanayake C, Kumla J, Karunarathna SC (2026) Two novel species belonging to *Psathyrella* sections *Atomatae* and *Hydrophilae* (Psathyrellaceae, Agaricales) from Yunnan Province, China, based on morphological and multi-locus phylogenetic analyses. MycoKeys 129: 1–22. https://doi.org/10.3897/mycokeys.129.179449

Introduction

Psathyrella (Fr.) Quél. was initially described as *Psathyra* Fr., a tribe of the genus *Agaricus* L. (Fries 1821, 1838), and was subsequently treated as a subgenus within Agaricaceae Chevall (Fries 1849). Quelet (1872) raised it to the genus *Psathyrella*. Later, Singer (1951, 1975) revised the two genera *Drosophila* Quél. and *Psathyrella*, and incorporated the *Drosophila* species into *Psathyrella*. Based on phenotypic characteristics, Kits van Waveren (1985) divided *Psathyrella* into two subgenera and 12 sections, primarily according to spore size: species with spores larger than 10 µm were assigned to subgenus *Psathyra*; otherwise, they were placed in subgenus *Psathyrella*, which contained five sections. Previously, studies of *Psathyrella* have mainly focused on Europe and North America (Kits van Waveren 1987; Hansen and Knudsen 1992; Örstadius and Huhtinen 1996), largely following the classification scheme proposed by Kits van Waveren (1985). In addition, new *Psathyrella* species have been reported from other regions, including South America (Guzmán et al. 1988) and Asia (Natarajan 1978; Zheng 1988; Ying 1994; Takahashi 2000), with these studies primarily based on morphological characteristics.

With the development of molecular biology, Redhead et al. (2001b) and Padamsee et al. (2008) placed *Psathyrella* within Psathyrellaceae Vilgalys, Moncalvo & Redhead, and phylogenetic studies have shown that the genus *Psathyrella* is not monophyletic (Keirle et al. 2004; Walther et al. 2005; Matheny et al. 2006; Padamsee et al. 2008). However, molecular phylogeny based on nrITS and nrLSU sequences failed to adequately distinguish species within *Psathyrella*. For instance, *P. conopilus* (Fr.) A. Pearson & Dennis clusters with species of *Parasola* Redhead, Vilgalys & Hopple with strong support (BS 99% and PP 1.00); *P. marcescibilis* (Britzelm.) Singer and *P. pannucioides* A.H. Sm. cluster with the *Coprinopsis* P. Karst. species (Larsson and Örstadius 2008). Consequently, several authors proposed wholesale realignment of the group (Redhead et al. 2001a, b; Gams 2002; Larsson and Örstadius 2008).

Nagy et al. (2013) conducted a phylogenetic analysis of the four-loci (nrITS, nrLSU, *tef*-1α, and *btub*) dataset, and Örstadius et al. (2015) reclassified the genus *Psathyrella* based on this analysis. Although not all species classifications were well supported, the conclusion still serves as the basis for the classification of the genus *Psathyrella* (Örstadius et al. 2015). Yan (2018) examined 769 samples from China and identified 46 *Psathyrella* species; the results showed that the taxonomic boundaries were consistent with the two subgenera defined by Kits van Waveren (1985). Voto (2020) elevated *Psathyrella* subsect. *Lutenses* Kits van Wav. (*P. lutensis*) to the sectional level by extracting it from *Psathyrella* sect. *Spadiceogriseae* Kits van Wav. and emended the definition of *Psathyrella* sect. *Spadiceogriseae*. Based on subsequent in-depth studies of numerous specimens, combined with morphological and phylogenetic analyses, Wächter and Melzer (2020) revised the Psathyrellaceae and divided *Psathyrella* into 18 subclades, *viz.*, sect. *Pennatae* (*P. pennata*), sect. *Cystopsathyra* (*P. kellermanii*), sect. *Noli-tangere* (*P. noli-tangere*), sect. *Hydrophilae* (*P. piluliformis*), sect. *Pygmaeae* (*P. pygmaea*), sect. *Saponaceae* (*P. saponacea*), sect. *Stridvalliorum* (*P. stridvallii*), sect. *Arenosae* (*P. arenosa*), sect. *Confusae* (*P. gordonii*), sect. *Obtusatae* (*P. obtusata*), sect. *Spadiceogriseae* (*P. spadiceogrisea*), sect. *Jacobssoniorum* (*P. jacobssonii*), sect. *Microrhizae* (*P. microrhiza*), sect. *Pseudostropharia* (*P. caput-medusae*), sect. *Lutenses* (*P. lutensis*), sect. *Psathyrella* (*P. gracilis*), sect. *Atomatae* (*P. prona*), sect.

Sinefibularum (*P. vinosofulva*) (Wächter and Melzer 2020). To date, excluding synonyms, variants, and varieties, Species Fungorum has recorded 674 *Psathyrella* species, with sequence data for at least half of them available in NCBI GenBank.

Psathyrella is a saprotrophic genus of fragile, hygrophanous agarics that leave a dark-brown spore deposit, invariably possess cheilocystidia, and exhibit the "fade-to-grey" reaction of basidiospores in concentrated H_2SO_4 (Kits van Waveren 1985; Örstadius et al. 2015; Wächter and Melzer 2020; Bhunjun et al. 2022). The species of *Psathyrella* most often occur on soil, wood, dung of cows and horses (Lange 1939; Smith 1972; Kits van Waveren 1985; Hansen and Knudsen 1992; Yan 2018). However, a few occur on old bonfires or in swamps (Pegler 1977; Kirk et al. 2008; Larsson and Örstadius 2008; Yan and Bau 2018a). Based solely on morphological studies, *Psathyrella* is similar to the genera *Candolleomyces* D. Wächt. & A. Melzer and *Kauffmania* Örstadius & E. Larss. (Örstadius et al. 2015; Wächter and Melzer 2020). However, *Candolleomyces* can be distinguished by the presence or absence of pleurocystidia (Wächter and Melzer 2020). In *Kauffmania*, only a single species has been recorded, similar to *Psathyrella*, and they cannot be distinguished by a single morphological feature (Örstadius et al. 2015; Wächter and Melzer 2020).

This study aims to describe two novel *Psathyrella* species from Yunnan Province, China, based on morphological and phylogenetic analyses. Detailed descriptions, illustrations, and phylogenetic results of the two new species are also provided.

Materials and methods

Sample collection and morphological observation

Fresh basidiomata were collected from Qujing City, Yunnan Province, China, in 2025. They were photographed *in situ*, and essential collection information was recorded (Rathnayaka et al. 2024). The basidiomata were placed in plastic collection boxes and taken to the mycology laboratory at Qujing Normal University. Macromorphological characteristics, such as pileus, lamella, and stipe, were recorded while the specimens were fresh. Color names and codes were based on the system developed by Kornerup and Wanscher (1978). The fresh specimens were dried at 40 °C in an electric oven (Hu et al. 2022). Dried specimens were sliced and mounted in a 5% KOH solution containing 1% Congo red solution for microstructure observation (Tarafder et al. 2025). The light Eclipse 80i microscope (Olympus, Japan) was used to view features of basidia, basidiospores, cystidia, and pileipellis, which were drawn using the drawing tube attached to the microscope. Micromorphological measurements were obtained using Adobe Photoshop 2019, with at least 40 sample data points for each structure. The basidiospore dimensions were reported as (a–) b–c (–d), where the range 'b–c' represented 90% or more of the measured value, and a and d are the extreme values. The meanings of "avL" and "avW" are average length and average width, respectively. The Q refers to the length/width ratio values of all measured basidiospores. Q_m refers to the average Q value with standard deviation. The dry specimens were deposited in the Herbarium of Guizhou Medical University, Guiyang (GMB-W), China. All line drawings of the microstructures were made freehand from rehydrated materials and subsequently modified in Adobe Photoshop 2019.

DNA extraction, PCR amplification, and sequencing

The genomic DNA was extracted from the lamellae of dried specimens using an Ezup Fungus Genomic DNA extraction kit (Sangon Biotech, Shanghai, China) according to the manufacturer's instructions. The primer pairs ITS1/ITS4, LR5/LR0R, and EF1-983F/EF1-2218R were used to amplify the internal transcribed spacer (nrITS) and partial large subunit (nrLSU) of ribosomal RNA and partial translation elongation factor 1-alpha (*tef*-1α) genes, respectively (Vilgalys and Hester 1990; White et al. 1990; Gardes and Bruns 1993; Örstadius et al. 2015). PCR amplification was performed in a 25 μL reaction volume containing 12.5 μL of 2 × Bench Top™ Taq Master Mix, 8.5 μL ddH_2O, 1 μL of each primer (10 μM), and 2 μL genomic DNA. The PCR thermal cycle programs for nrITS and nrLSU amplification were based on those described by Zheng et al. (2025), and the *tef*-1α cycle programs followed those described by Yan and Bau (2018a). After PCR amplification, the purification and sequencing of PCR products were completed by Sangon Biotech Engineering Technology (Shanghai) Co., Ltd. (Shanghai, China). The name of the new taxon was registered in Index Fungorum (2026) (https://www.indexfungorum.org/Names/IndexFungorumRegister.htm). All newly generated sequences in this study were deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank/) and listed in Table 1.

Phylogenetic analyses

The assembly of the forward and reverse primers for the recently obtained sequences was accomplished using BioEdit version 7.0.5.3 and SeqMan version 7.0.0 software packages (DNASTAR, Madison, WI) (Plasterer 1997; Hall 1999). According to the latest studies, additional *Psathyrella* sequences were obtained from GenBank for phylogenetic analyses (Örstadius et al. 2015; Bau and Yan 2021a; Muñoz et al. 2022; Table 1). The sequences were aligned using the online multiple alignment program MAFFT version 7 (Katoh and Standley 2016; Katoh et al. 2019), followed by automatic trimming using TrimAl v. 1.3 with the gappyout method (0.4) (Katoh et al. 2019). Subsequently, the combined FASTA files of nrITS, nrLSU, and *tef*-1α sequences were converted to PHYLIP and NEXUS formats using the online Alignment Transformation Environment (https://www.sing-group.org/ALTER/) (Glez-Peña et al. 2010). Phylogenetic tree construction for both Maximum Likelihood (ML) and Bayesian Inference (BI) analyses was conducted on the CIPRES Science Gateway online platform (https://www.phylo.org/portal2/home.action) (Miller et al. 2012). ML analysis of the dataset was performed on the above platform using RAxML-HPC v.8 on ACCESS with the GTRGAMMA substitution model and 1,000 bootstrap replicates (Stamatakis et al. 2005; Stamatakis 2006, 2014). BI analysis was performed using MrBayes on XSEDE v3.2.7a (Ronquist et al. 2012), with six simultaneous Markov chains running for 2,000,000 generations, sampling every 200th generation. The best-fitting model of sequence evolution (GTR+I+G) was determined using MrModelTest 2.2 (Nylander 2004). Topologies sampled below the 25% asymptote were excluded from the burn-in procedure. The phylogenetic trees were visualized and edited with FigTree v1.4.0 (Rambaut and Drummond 2012), and the final figure layouts were created in Adobe Illustrator CC 2021.

Table 1. Names, voucher numbers, and corresponding GenBank accession numbers of the taxa used in the phylogenetic analysis.

Taxon	Voucher number	Locality	GenBank accession number		
			nrITS	nrLSU	*tef*-1α
Candolleomyces candolleanus	LAS73030	Sweden	KM030175	KM030175	/
Ca. candolleanus	LÖ38-00	Sweden	DQ389720	DQ389720	/
Ca. shennongdingicus	HMAS 258917	China	OR822165	OR822147	OR819984
Ca. shennongdingicus^{T}	HMAS 258918	China	OR822166	OR822148	OR819985
Ca. sichuanicus^{T}	HMAS 287616	China	PP734617	PP734628	PP729330
Ca. sichuanicus	HMAS 287617	China	PP734618	PP734629	PP729331
Ca. subcacao^{T}	HMJAU37807	China	MW301064	MW301092	MW314081
Ca. subminutisporus^{T}	HMJAU37801	China	MW301066	MW301094	MW314083
Coprinopsis cineraria^{T}	CBM-FB-24142	Japan	KC992962	/	/
Co. uliginicola^{T}	Smith34903	USA	KC992960	KC992960	/
Psathyrella agrariella	MICH65241	USA	MF325951	/	/
P. albescens	MCVE29106	Italy	MF325953	/	MF521822
P. albescens	MCVE29107	Italy	MF326009	/	/
P. almerensis	LO379-06	Sweden	KC992873	KC992873	KJ732768
P. almerensis	LO31-04	Sweden	KC992874	KC992874	/
P. ammophila	SZMC-NL-1450	Hungary	FN396111	FN396162	FN396218
P. ammophila	LO359-11	Sweden	KC992872	KC992872	KJ732767
P. bifrons	CBS:299.47	France	MH856259	MH867794	/
P. carinthiaca^{T}	MCVE25611	Austria	MF325963	/	/
P. carinthiaca	VER fu19	Slovenia	OQ296568	/	OQ687051
P. carminei	LO5-09	Italy	KC992880	KC992880	KJ732773
P. clivensis	LO182-03	Sweden	DQ389683	DQ389683	KJ732774
P. clivensis	SZMC-NL-1952	Hungary	FM163228	FM160681	FM897216
P. corrugis	SZMC-NL-1951	Hungary	FM878015	FM876272	FM897220
P. dicrani	LO207-04	Sweden	DQ389698	/	/
P. fagetophila	SZMC-NL-2530	Hungary	FM878003	FM876259	FM897222
P. fatua	LO132-97	Sweden	DQ389681	/	/
P. fatua	LO231-08	Sweden	KC992879	KC992879	KJ732772
P. fimiseda^{T}	GB LO56-96	USA	NR_158879	/	/
P. fusca	SZMC-NL-0630/2157	Hungary	FM878030	FM876288	FM897217
P. fusca	LO287-04	Sweden	KC992892	KC992892	KJ732779
P. griseovelata	GM2055	Spain	MZ571481	MZ604935	/
P. griseovelata	GM2495	Spain	MZ571482	MZ604936	/
P. impexa	LO78-93	Sweden	KC992900	/	/
P. kitsiana^{T}	GB LO217-85	USA	NR_158878	/	/
P. lilliputana	LO130-09	Sweden	KC992850	KC992850	KJ732756
P. lilliputana	GB LO130-09	Sweden	NR_167949	/	/
P. lutulenta	AH21379	Spain	KC992875	KC992875	/
P. mammifera	HMJAU 37882	China	MG734740	/	/
P. marquana	AM1693	Germany	MF668178	MF668178	/
P. merdicola^{T}	GB LO45-02	Sweden	NR_158877	/	/
P. microrhiza	SZMC-NL-3059	Hungary	FN396130	FN396178	FN396230
P. mycenoides	HMJAU37993	China	MG734731	/	/
P. mycenoides	HMJAU37888	China	MG734730	/	/
P. noli-tangere	LÖ83-03	Sweden	DQ389713	DQ389713	FN396239
P. oboensis	HMJAU37936	China	MT429164	MW413366	/
P. oboensis	SFSU DED-8234	São Tomé	NR_148107	/	/

Taxon	Voucher number	Locality	GenBank accession number		
			nrITS	nrLSU	*tef*-1α
P. orbicularis	LO149-11	Sweden	KC992897	/	KJ732786
P. orbicularis	LO211-04	Sweden	DQ389692	/	/
P. owyheensis	HMAS 292422	China	OR237033	/	/
P. owyheensis	MICH5357	USA	MF325990	/	/
P. panaeoloides	LO44-03	Sweden	DQ389719	DQ389719	KJ732782
P. pertinax	LO259-91	Sweden	DQ389701	DQ389701	KJ732809
P. pertinax	HMJAU 6830	China	MG734735	/	/
P. pervelata	SZMC-NL-1950	Hungary	FN430694	FN396192	FM897221
P. phegophila	SZMC-NL-3527	Hungary	FN396129	FN396198	FN396229
P. piluliformis	XC23-242	France	PV121594	PV121907	/
P. piluliformis	SZMC-NL-3923	Hungary	FN396136	FN396185	FN396235
P. piluliformoides	HMJAU37923	China	MW405106	MW413362	MW411002
P. potteri	AH33721	Spain	MF966495	MF962872	/
P. prona	LÖ237-00	Sweden	KJ939634	/	/
P. pseudogracilis	SZMC-NL-2142	Hungary	FM878025	FM876283	FM897249
P. pygmaea	SZMC-NL-2325	Hungary	FM878011	FM876267	FM897224
***P. qujinguniversitatica*[T]**	**GMB-W1229**	**China**	**PX443606**	**PX443617**	**PX583848**
P. qujinguniversitatica	**GMB-W1230**	**China**	**PX443607**	**PX443618**	**PX583849**
P. rogersiae[T]	MCVE29120	Italy	MF325995	/	/
P. romagnesii	LO85-98	Sweden	DQ389716	/	/
P. sacchariolens	SZMC-NL-3995	Hungary	FN396133	FN396182	FN396233
P. scanica[T]	GB LO183-09	Sweden	NR_167957	/	/
P. scatophila[T]	LO64-95	Sweden	DQ389703	/	/
P. seminuda[T]	Smith34091	USA	KC992907	/	/
P. senex	LÖ115-02	Germany	DQ389712	DQ389712	/
P. spadiceogrisea	MCVE29103	France	MF325997	/	MF521779
P. spadiceogrisea	LO102-98	Sweden	KC992878	KC992878	KJ732771
P. squamosa	HMJAU37816	China	MG367206	/	/
P. squamosa	LO104-95	Sweden	DQ389687	/	/
P. tintinnabula	HMLD2497	China	MK123930	/	/
P. tintinnabula[T]	HFJAU0711	China	MK123929	MK211206	/
P. umbrina	SZMC-NL-1949	Hungary	FM878004	FM876260	FM897226
P. velatipes	MICH12106	USA	MF326004	/	MF521774
P. vestita	SZMC-NL-2346	Hungary	FN430693	FM876260	FN430696
P. warrenensis	KA16-1043	Kyrgyzstan	MK351682	/	/
P. warrenensis	Smith70162	USA	KC992906	/	/
***P. yunnanensis*[T]**	**GMB-W1231**	**China**	**PX443608**	**PX443619**	**PX583850**
P. yunnanensis	**GMB-W1232**	**China**	**PX443609**	**PX443620**	**PX583851**

Notes: The newly generated sequences in this study are in bold; superscript "T" represents the type species; and "/" indicates unavailable sequences.

Results

Phylogenetic analyses

The combined nrITS, nrLSU, and *tef*-1α sequences were used to assess phylogenetic relationships among *Psathyrella* species. *Coprinopsis cineraria* (Har. Takah.) Örstadius & E. Larss. (CBM-FB-24142[T]) and *Co. uliginicola* (McKnight & A.H. Sm.) Örstadius & E. Larss. (Smith34903[T]) were used as the outgroup (Bau and Yan 2021a). The final concatenated dataset of nrITS, nrLSU, and *tef*-1α sequences, consisting of 85 nrITS, 50 nrLSU, and 42 *tef*-1α sequences, was used to conduct ML

and BI analyses. The phylogenetic trees generated by ML and BI were similar, and the results were consistent with those of previous studies by Yan (2018) and Wächter and Melzer (2020). Therefore, the phylogenetic tree obtained from ML analysis was chosen for presentation in Fig. 1. The RAxML tree was based on a combined dataset of nrITS, nrLSU, and *tef*-1α gene sequence data, which comprised 2,658 characters (LSU: 1–900, ITS: 901–1,656, *tef*-1α: 1,657–2,658), including gaps. The best-scoring RAxML tree with a final likelihood value of -19568.188807 is presented. Estimated base frequencies were as follows: A = 0.253834, C = 0.231013, G = 0.254215, T = 0.260938; substitution rates AC = 1.383986, AG = 2.887342, AT = 1.622628, CG = 0.727172, CT = 6.064389, GT = 1.000000.

In the phylogeny, our collections GMB-W1229^{T} and GMB-W1230 (*Psathyrella qujinguniversitatica*) were placed in *Psathyrella* sect. *Atomatae* Romagn. ex Singer and formed a distinct lineage closely related to *P. lilliputana* Örstadius & E. Larss. (LO130-09), with strong statistical support (99% BS and 1.00 PP; Fig. 1). The collections GMB-W1231^{T} and GMB-W1232 (*P. yunnanensis*), belong to *Psathyrella* sect. *Hydrophilae* Romagn. ex Singer and form a distinct lineage closely related to *P. carinthiaca* Voto (MCVE 25611^{T}) and *P. piluliformis* (Bull.) P.D. Orton (SZMC-NL-3923) being separated with statistical support of 98% BS and 1.00 PP (Fig. 1). Based on nucleotide comparisons, *P. qujinguniversitatica* (GMB-W1229^{T}) is different from *P. lilliputana* (LO130-09) by 38/622 bp (6.11%, without gap) of the nrITS, for nrLSU by 19/848 bp (2.24%, without gap), and by 97/661 bp (14.67%, without gap) of the *tef*-1α. *Psathyrella yunnanensis* (GMB-W1231^{T}) is different from *P. piluliformis* (SZMC-NL-3923) by 35/641 bp (5.46%, without gap) of the nrITS, for nrLSU by 26/798 bp (3.26%, without gap), and by 40/1,048 bp (3.82%, without gap) of the *tef*-1α. In addition, *P. yunnanensis* (GMB-W1231^{T}) is different from *P. carinthiaca* (MCVE 25611^{T}) by 25/639 bp (3.91%, without gap) of the nrITS and by 37/1,063 bp (3.91%, without gap) of the *tef*-1α (compared with *P. carinthiaca* VER fu19).

Taxonomy

***Psathyrella qujinguniversitatica* D.G. Zheng. & Karun., sp. nov.**

Index Fungorum: IF904677

Figs 2a–c, 3

Etymology. Refers to 'Qujing Normal University', where the holotype was collected.

Holotype. China • Yunnan Province, Qujing City, Qujing Normal University, on grassland, 25°31'29"N, 103°44'39"E, elev. 1,882 m, 23 June 2025, D.G. Zheng (QJ25-05 = GMB-W1229).

Description. ***Pileus*** 4–6 mm in diameter, hemispherical when young and parabolic to broadly parabolic when mature, hygrophanous, beige (4C3) to light brown (5D4) at the center and yellowish gray (4B2) to grayish beige (4C2) towards the margin, smooth, faintly visible striations at the margin, with granules or powder on the surface of the pileus. ***Veil*** fibrillose, gradually disappearing in maturity stages. ***Lamellae*** adnexed to adnate, regular, yellowish gray (4B3–4). ***Stipe*** 21–30 × 0.3–0.4 mm, fragile, cylindrical, hollow, slender, equal, from the top to the base, the color gradually deeper from white (5A1) to light brown (5D5), without visible mycelium at the base. ***Annulus*** absent. ***Odour and taste*** were not determined.

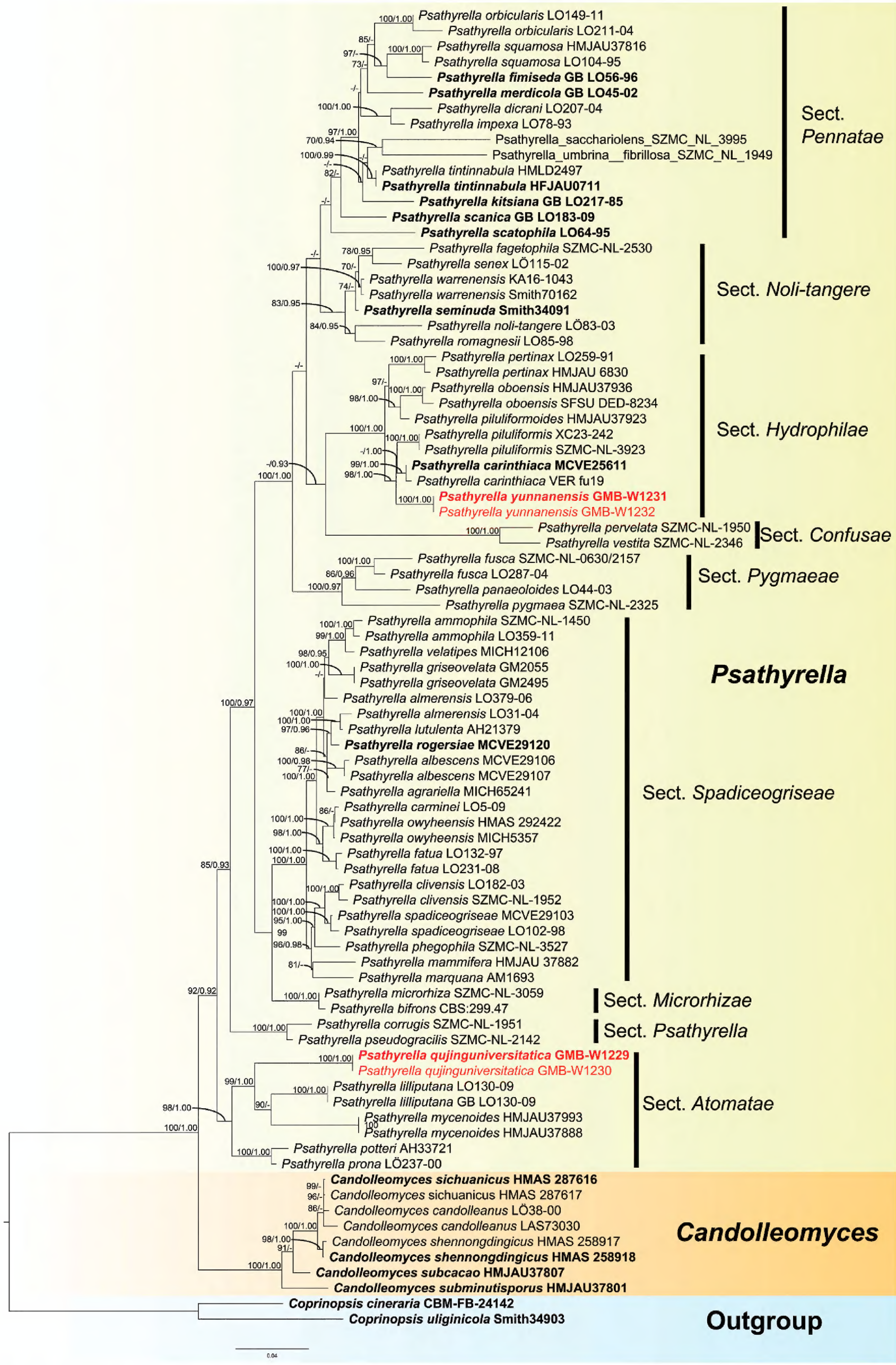

Figure 1. Phylogenetic tree for *Psathyrella* generated from the combined sequence dataset (nrITS, nrLSU, and *tef*-1α) using Maximum Likelihood (ML) analysis and Bayesian Inference (BI) analyses. The ML bootstrap values ≥ 70% and BI posterior probabilities ≥ 0.90 are provided at relevant nodes (BS/PP). The new species are in red text. Type species are in bold.

Figure 2. Basidiomata of *Psathyrella qujinguniversitatica* (GMB-W1229, holotype) (**a–c**), and *Psathyrella yunnanensis* (GMB-W1231, holotype) (**d–f**). Scale bars: 1 cm (**a, b, d–f**); 1 mm (**c**).

Basidiospores (9.0–)9.7–11.3(–12.4) × (5.1–)5.6–6.7(–7.1) µm (avL = 10.4 µm, avW = 6.2 µm), Q = 1.46–1.90, Q_m = 1.69 ± 0.15, ellipsoid to oblong, pale brown to brown in water, deepening in 5% KOH, smooth, with germ pore central or slightly eccentric, 1.0–1.5 µm broad, and many canary yellow (2B7) oil drops. ***Basidia*** (17.3–)18.0–21.8(–24.1) × (6.6–)6.8–8.4(–8.8) µm, clavate, hyaline, 2- or 4-spored, occasionally 1-spored. ***Pleurocystidia*** (27.0–)27.7–41.9(–42.4) × (7.8–)10.1–14.7(–17.0) µm, scattered to rare, lageniform to fusiform, pyriform or utriform, thin-walled, not forked, with obtuse apex. ***Cheilocystidia*** (20.0–)25.2–35.2(–50.3) × (4.5–)5.6–9.6(–12.3) µm, numerous, utriform, pyriform, cylindrical to claviform, lageniform, partially thick-walled, hyaline. ***Pileipellis*** a one- to two-layered irregular epithelium composed of globose to subglobose or ellipsoid cells 22–38 × 18–32 µm, thin-walled, hyaline

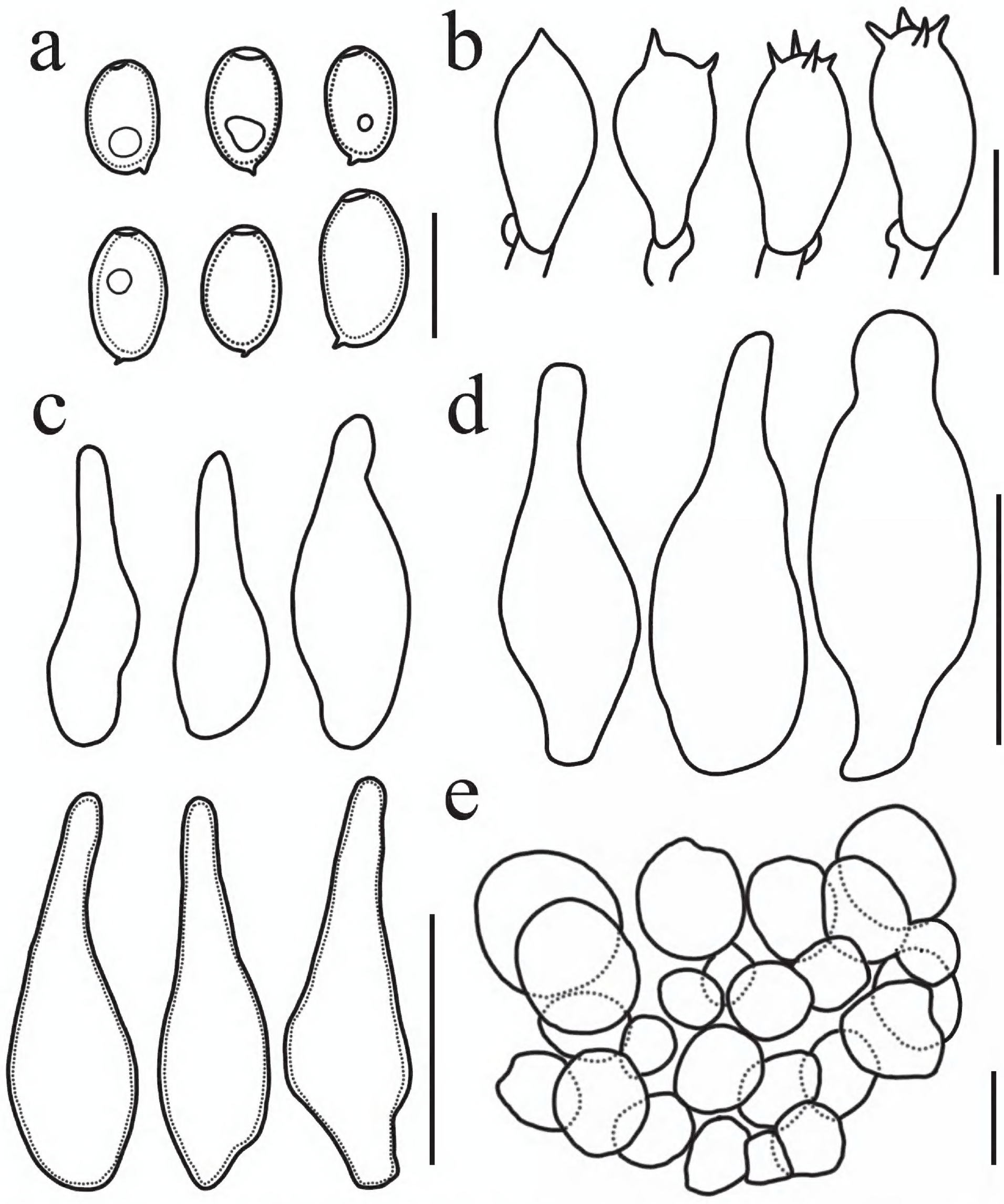

Figure 3. *Psathyrella qujinguniversitatica* (GMB-W1229, holotype). **a.** Basidiospores; **b.** Basidia; **c.** Cheilocystidia; **d.** Pleurocystidia; **e.** Pileipellis. (Micrographs are provided in Suppl. material 1: fig. S1). Scale bars: 10 µm (**a, b**), 20 µm (**c–e**).

in 5% KOH. ***Stipitipellis*** a cutis of parallel, slightly skewed, cylindrical, smooth hyphae, thin-walled, 5–12 µm wide. ***Clamp connection*** present.

Habitat. Solitary or gregarious in a grassland at Qujing Normal University in Yunnan Province, China.

Distribution. Only known from Yunnan, China.

Additional specimen examined. China • Yunnan Province, Qujing City, Qujing Normal University, on grassland, 25°31'36"N, 103°44'49"E, elev. 1,889 m, 23 June 2025, D.G. Zheng & S.C. Karunarathna (QJ25-80 = GMB-W1230, isotype).

GenBank numbers. GMB-W1229: nrITS = PX443606, nrLSU = PX443617, *tef*-1α = PX583848. GMB-W1230: nrITS = PX443607, nrLSU = PX443618, *tef*-1α = PX583849.

Notes. In morphology, *P. qujinguniversitatica* differs from *P. lilliputana* by larger basidiomata, especially longer stipes (21–30 × 0.3–0.4 mm vs. 6–8 × 0.2–0.5 mm), longer basidia (18.0–21.8 × 6.8–8.4 µm vs. 16–19 × 8–9 µm), and slightly larger pileipellis cells (18–38 µm vs. 15–30 µm) (Örstadius et al. 2015). In addition, *P. lilliputana* is coprophilic and differs in having a semiglobate to convex pileus that is reddish-brown, and the stipe apex is pulverulent, with sparsely fibrillose veil remnants. In micromorphology, it can be easily distinguished from our species by its rarely forked pleurocystidia and cheilocystidia, and yellowish-red basidiospores, which are sometimes snout-like at the apex or irregular in outline (Örstadius et al. 2015). In the phylogenetic tree, *P. qujinguniversitatica* is closely related to *P. lilliputana* and *P. mycenoides* T. Bau. Their basidiomata are all less than 5.0 mm. However, *P. mycenoides* differs in having smaller basidia and a dirty white to pinkish pileus (Örstadius et al. 2015; Yan and Bau 2018a). Based on the above evidence, we identify our collection as *P. qujinguniversitatica* sp. nov.

***Psathyrella yunnanensis* D.G. Zheng. & Karun., sp. nov.**

Index Fungorum: IF904678

Figs 2d–f, 4

Etymology. "*yunnanensis*" refers to the type locality, Yunnan Province, China.

Holotype. China • Yunnan Province, Qujing City, Malong County, on humus-rich soil among moss and woody debris, 25°18'57"N, 103°16'03"E, elev. 2,152 m, 12 July 2025, D.G. Zheng (MLX74 = GMB-W1231).

Description. ***Pileus*** 26–35 mm in diameter, parabolic or subumbonate when young, and subumbonate or convex when mature, slightly hygrophanous, brownish orange (6C5) at the center, the color gradually paler between the center and edges, but deeper at the edges, which are light brown (6D6) to brown(6E6) towards the margin, smooth, striations distinct at margin. ***Veil*** white (5A1), fibrillose, rarely on the edge of the pileus, and gradually disappearing in maturity stages. ***Lamellae*** adnexed to adnate, even, regular and with tiers, dull red (9C4) to reddish brown (9D4). ***Stipe*** 69–79 × 6–7 mm, fragile, fistulose, cylindrical, hollow, flexuous, longitudinally fibrillose or flocculose, slightly thickened towards the middle, white (5A1) to white gray (5B1), with a little white mycelial tomentum at the base. ***Annulus*** absent. ***Odor and taste*** were not determined.

Basidiospores (5.8–)6.4–8.1(–9.5) × (2.9–)3.2–4.4(–5.8) µm (avL = 7.28 µm, avW = 3.90 µm), Q = 1.45–2.03, Q_m = 1.87 ± 0.27, ellipsoid to oblong, slightly flexuous or irregular in outline, thick-walled, base often broadly truncate, pale brown to brown in water, and deepening in 5% KOH, smooth, with germ pore absent or partially present with medium guttules. ***Basidia*** (20.4–)25.2–32.6(–35.2) × (5.8–)6.3–8.3(–9.2) µm, clavate, hyaline, 4- or 2-spored, with granular content, have basidioles arranged in a regular pattern. ***Pleurocystidia*** (32–)44.0–62.8(–71.6) × (6.4–)9.04–18.0(–22.6) µm, abundant, narrowly clavate

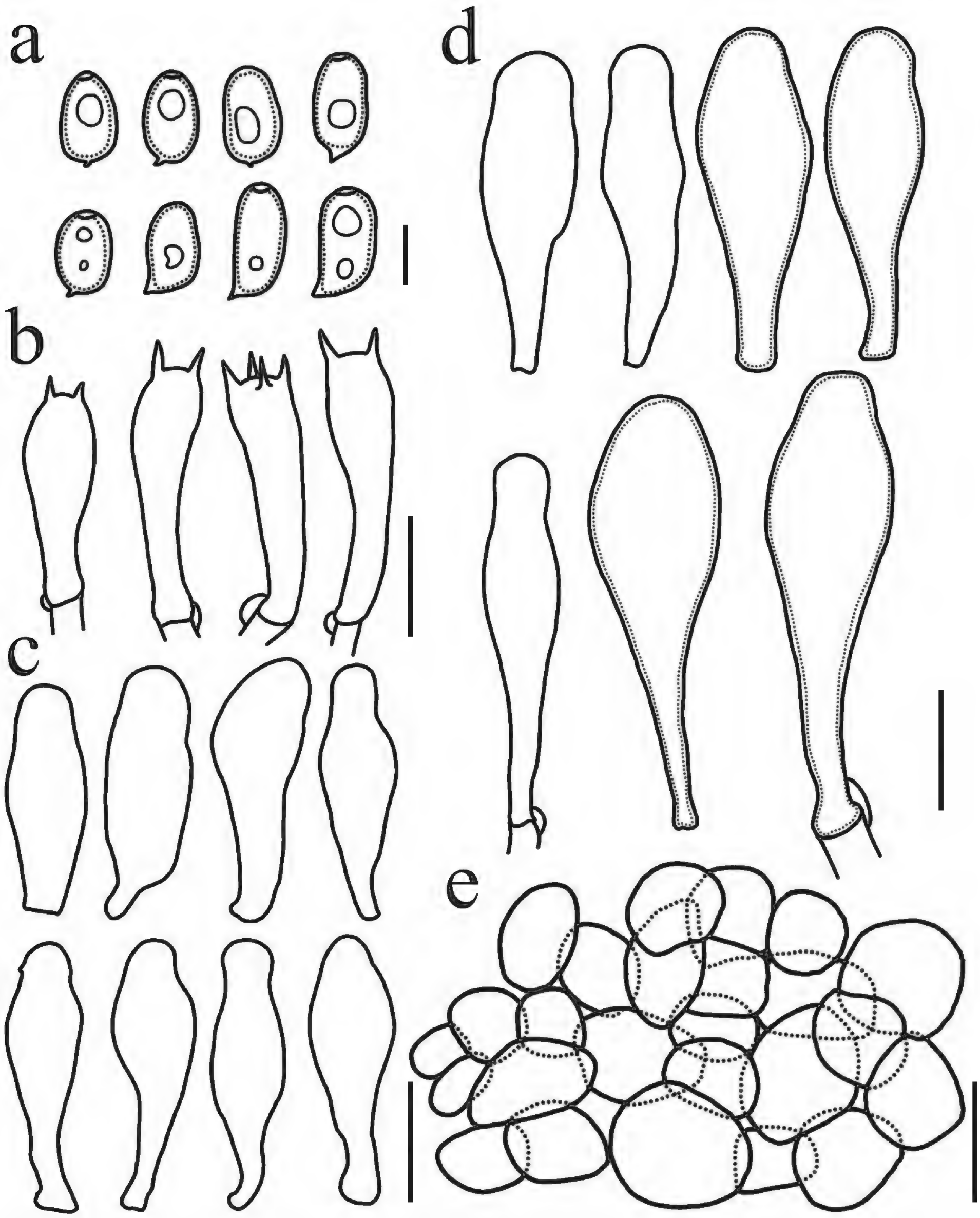

Figure 4. *Psathyrella yunnanensis* (GMB-W1231, holotype). **a.** Basidiospores; **b.** Basidia; **c.** Cheilocystidia; **d.** Pleurocystidia; **e.** Pileipellis. (Micrographs are provided in Suppl. material 1: fig. S2). Scale bars: 5 μm (**a**); 20 μm (**b–d**); 10 μm (**e**).

to clavate, or narrowly utriform to utriform, thick-walled, apex broadly obtuse, dissolving in 5% KOH. ***Cheilocystidia*** (28.1–)33.1–46.7(–49.4) × (7.5–)10.1–14.8(–15.9) μm, utriform, oblong to claviform, partially thin-walled, hyaline. ***Pileipellis*** a one- to two-layered irregular epithelium composed of globose to sub-

globose or ellipsoid cells 28–40 × 18–39 µm, thin-walled, hyaline in 5% KOH. ***Stipitipellis*** a cutis of parallel, slightly skewed, cylindrical, smooth hyphae, thin-walled, 7–12 µm wide. ***Clamp connection*** present.

Habitat. Scattered or gregarious on humus-rich soil among moss and woody debris.

Distribution. Only known from Yunnan, China.

Additional specimen examined. CHINA • Yunnan Province, Qujing City, Malong County, on humus-rich soil among moss and woody debris, 25°18'57"N, 103°16'03"E, elev. 2,152 m, 12 July 2025, D.G. Zheng & S.C. Karunarathna (MLX126 = GMB-W1232, isotype).

GenBank numbers. GMB-W1231: nrITS = PX443608, nrLSU = PX443619, *tef*-1α = PX583850. GMB-W1232: nrITS = PX443609, nrLSU = PX443620, *tef*-1α = PX583851.

Notes. In morphology, *P. yunnanensis* differs from *P. piluliformis* by smaller basidiomata, especially the narrower pileus (25–35 mm vs. 30–70 mm), larger basidia (25.2–32.6 × 6.3–8.3 µm vs. 15–22 × 5.0–8.0 µm), and larger basidiospores (6.4–8.1 × 3.2–4.4 µm vs. 5.0–6.5 × 3.5–4.0 µm). It is also distinguished by its fibrillose veil, basidioles arranged in a regular pattern, and pale brown to brown basidiospores. *Psathyrella piluliformis* has a pileus that is brown to reddish brown or honey brown, hygrophanous, with blunt, rounded protrusions in the center, and faint, translucent stripes along the edge (Yan 2018; Kuo 2020). *Psathyrella yunnanensis* differs from *P. carinthiaca* in having a lighter-colored pileus, larger pleurocystidia (44.0–62.8 × 9.0–18.0 µm vs. 30–45 × 8.0–13.7 µm), larger cheilocystidia (33.1–46.7 × 10.1–14.8 µm vs. 17–37 × 8–12 µm), and larger basidia (25.2–32.6 × 6.3–8.3 µm vs. 10–18 × 5–7 µm). In contrast, *P. carinthiaca* is characterized by a reddish-brown to brick-red or brownish (pinkish-) violaceous pileus, blackish violaceous lamellae, and smaller basidiospores (5.0–6.0 × 3.0–3.7 µm vs. 6.4–8.1 × 3.2–4.4 µm) (Voto 2011; Voto et al. 2020). *Psathyrella pertinax* (Fr.) Örstadius has a pileus color ranging from reddish brown to ochraceous brown to yellow brown, and the pileus often becomes radially rugose, veined, or reticulate (Örstadius 2007). The main identifying feature of *P. oboensis* Desjardin & B.A. Perry is that the gills are extremely dense, slender, and 1.0–1.5 mm wide (Desjardin and Perry 2016). Based on the above evidence, we identify our collection as *P. yunnanensis* sp. nov.

Discussion

In this study, two new species exhibit all micromorphological characteristics consistent with the genus *Psathyrella*; notably, the presence of pleurocystidia is a key diagnostic feature distinguishing it from the genus *Candolleomyces*. Based on molecular data and morphological features, our two novel species are respectively accommodated in *Psathyrella* sect. *Atomatae* and sect. *Hydrophilae*. In the classification criteria of Wächter and Melzer (2020), *Psathyrella* sect. *Atomatae* is characterized by its very small to medium-sized basidiomata that are terrestrial or coprophilous, a drying pileus that is often with pink tones, large, dark basidiospores with a centrally located germ pore, 1-, 2- or 4-spored basidia, the cheilocystidia predominantly lageniform, subutriform or clavate, and rarely pleurocystidia. Compared with other species in *Psathyrella* sect. *Atomatae*, *P. qujinguniversitatica* can usually be distinguished by its small basidiomata, beige or light brown pileus,

and large basidiospores. Our species, *P. qujinguniversitatica*, meets all the characteristics of *Psathyrella* sect. *Atomatae* and forms an independent lineage in the phylogenetic tree (Fig. 1). This section has only one species recorded in China, *P. mycenoides*, which was described as a new species from Jilin Province. The proportion of species in *Psathyrella* sect. *Atomatae* found in China, compared to the global total, is 11% (Yan and Bau 2018a; Wächter and Melzer 2020).

Psathyrella sect. *Hydrophilae* is characterized by its small to medium-sized basidiomata that are all lignicolous; the veil is sparse to strongly developed; small, phaseoliform basidiospores without germ pores or indistinct germ pore; the marginal cells are lageniform, utriform, very often mucronate in the lamellar edge; and with moderately numerous clavate and sphaeropedunculate cells (Yan 2018; Wächter and Melzer 2020; Bau and Yan 2021a). Our new species, *P. yunnanensis*, meets the requirements of the above classification. However, our specimens were collected from humus-rich soil among moss and woody debris, rather than from the tree or wood itself. Moreover, in 2018, Yan recorded a specimen of *P. piluliformis* that was collected from the ground in a broadleaf forest in Heilongjiang Province, China (Yan 2018). This specimen also belongs to this section, but it was found growing in soil rather than lignicolous. In 2021, Bau and Yan (2021a) collected a new species, *P. piluliformoides*, which grew solitarily on moss and belongs to *Psathyrella* sect. *Hydrophilae*. This pattern may be associated with variations in geographical environments. The occurrence of these species suggests that the current circumscription of *Psathyrella* sect. *Hydrophilae* may not adequately reflect their ecological diversity (Padamsee et al. 2008; Bau and Yan 2021a). In particular, the habitat of *Psathyrella* sect. *Hydrophilae* is not confined to dead wood or other lignicolous substrates, but also encompasses humus-rich soils. This broader ecological amplitude indicates that the habitat range of *Psathyrella* sect. *Hydrophilae* is more diverse than previously assumed, and the possible existence of additional subsections within *Psathyrella* sect. *Hydrophilae*, underscoring the need for additional collections and data to better define its taxonomic characteristics. New species in *Psathyrella* sect. *Hydrophilae* continue to be discovered, and comprehensive datasets, including morphological characteristics, geographical distributions, and phylogenetic analyses, are being compiled. Although our new species, *P. yunnanensis*, has a different habitat, there is no doubt that it belongs to *Psathyrella* sect. *Hydrophilae*, from a phylogenetic and taxonomic point of view. This new information not only helps clarify the phylogenetic relationships among species within the sections but also provides key evidence for revising and improving the classification standards of the subgroup and for defining interspecies boundaries. In China, a total of four species from *Psathyrella* sect. *Hydrophilae* have been recorded, including one novel species, *P. piluliformoides* T. Bau & J.Q. Yan, representing 44% of the global diversity of this section (Wächter and Melzer 2020; Bau and Yan 2021a).

Before 2015, a total of 44 *Psathyrella* species had been reported from China. Yan (2018) re-examined these records and confirmed that 11 species were actually distributed within *Psathyrella*. Since then, continuous taxonomic investigations have considerably expanded the diversity of this genus in China, increasing the number of recorded species in China to 53 (Bi 1991; Mao 1997; Chang et al. 2006; Wang and Bau 2014; Wei 2017; Yan 2018; Cen et al. 2021; Bau and Yan 2021a, 2021b; Yan and Bau 2021; Li et al. 2023; Liang et al. 2023; Wang et al. 2024; Zhang 2024; Table 2). Notably, 11

Table 2. List of sections, species, and provinces of distribution of *Psathyrella* recorded in China.

Sections	Species	Provinces of distribution	References
Atomatae	*Psathyrella mycenoides*	Jilin	Yan (2018); Yan and Bau (2018a)
	P. qujinguniversitatica	Yunnan	This study
Confusae	*P. gordonii*	Jilin	Yan (2018); Yan and Bau (2017)
Hydrophilae	*P. oboensis*	Yunnan	Yan (2018); Liang et al. (2023)
	P. pertinax	Jilin	Yan (2018)
	P. piluliformis	Liaoning, Heilongjiang, Fujian, Guangdong, Yunnan, Sicuang, Hunan, Jilin, Xinjiang, Shanxi, Xizang, Hong Kong, Taiwan	Cen et al. (2021); Li et al. (2023); Wang and Bau (2014); Yan (2018)
	P. piluliformoides	Yunnan, Jilin	Yan (2018); Bau and Yan (2021a)
	P. yunnanensis	Yunnan	This study
Lutenses	*P. lutensis*	Neimenggu	Yan (2018)
Microrhizae	*P. boreifasciculata*	Neimenggu, Jilin, Heilongjiang	Yan (2018); Yan and Bau (2017)
	P. microrhiza	Ningxia	Mao (1997)
	P. owyheensis	Beijing	Wang et al. (2024)
Noli-tangere	*P. amygdalinospora*	Sicuang	Yan (2018); Bau and Yan (2021a)
	P. fennoscandica	Heilongjiang	Yan (2018)
	P. senex	Neimenggu, Jilin	Yan (2018); Yan and Bau (2017)
	P. subterrestris	Jilin, Hubei	Yan (2018)
Obtusatae	*P. obtusata*	Ningxia, Liaoning, Hong Kong, Neimenggu, Jilin, Sicuang	Mao (1997); Yan (2018)
Pennatae	*P. alpina*	Yunnan, Jiangxi	Yan (2018); Yan and Bau (2018b)
	P. borealis	Neimenggu, Jilin	Yan (2018)
	P. conica	Jilin	Yan (2018); Yan and Bau (2018a)
	P. jilinensis	Jilin	Yan (2018); Yan and Bau (2018a)
	P. pennata	Ningxia	Mao (1997)
	P. rostellata	Xinjiang	Yan (2018)
	P. spintrigeroides	Jilin	Yan (2018)
	P. squamosa	Hebei, Beijing, Neimenggu, Jilin, Heilongjiang, Liaoning, Guangdong, Ningxia	Yan (2018); Wang and Bau (2014); Wang et al. (2024); Cen et al. (2021); Wei (2017); Mao (1997)
	P. tintinnabula	Yunnan	Yan et al. (2019)
	P. vesterholtii	Sicuang	Yan (2018)
Psathyrella	*P. atomata*	Gansu	Zhang (2024)
	P. bipellis	Gansu, Jilin, Yunnan, Hebei	Zhang (2024); Wang et al. (2024); Yan (2018)
	P. corrugis	Gansu, Guangdong, Fujian, Sicuang, Neimenggu	Zhang (2024); Wang and Bau (2014); Yan (2018)
	P. longicauda	Ningxia	Li et al. (2023)
Pygmaea	*P. squarrosa*	Guangdong	Yan (2018); Yan and Bau (2021)
	P. truncatisporoides	Zhejiang	Yan (2018); Bau and Yan (2021a)
Pygmaeae	*P. amaura*	Jilin, Sicuang, Beijing	Yan (2018); Wang et al. (2024)
	P. olympiana	Jilin, Liaoning, Gansu, Beijing, Hebei	Cen et al. (2021); Zhang (2024); Wang et al. (2024)
	P. pygmaea	Jilin, Liaoning	Cen et al. (2021)
Saponaceae	*P. panaeoloides*	Xizang, Jilin	Yan (2018); Yan and Bau (2021)
	P. saponacea	Shanxi	Yan (2018); Yan and Bau (2021)
Sinefibularum	*P. effibulata*	Jilin	Yan (2018)

Sections	Species	Provinces of distribution	References
Spadiceogriseae	*P. bifrons*	Liaoning	Cen et al. (2021)
	P. carmine	Gansu, Neimenggu	Zhang (2024); Yan (2018)
	P. mammifera	Jilin, Sicuang	Yan (2018)
	P. marquana	Gansu	Zhang (2024)
	P. phegophila	Beijing	Wang et al. (2024)
	P. spadiceogrisea	Guangdong, Guizhou, Liaoning	Cen et al. (2021)
	P. subspadiceogrisea	Jilin	Yan and Bau (2017)
Un-placement section	*P. armeniaca*	Fujian, Guangdong, Liaoning	Cen et al. (2021); Wei (2017)
	P. campestris	Guangdong, Hebei, Henan, Liaoning, Yunnan	Cen et al. (2018); Yan and Bau (2017)
	P. lactobrunnescens	Yunnan	Liang et al. (2023)
	P. microspore	Jilin, Sicuang	Wang and Bau (2014)
	P. multissima	Jilin, Yunnan	Chang et al. (2006); Liu et al. (2020)
	P. rubiginosa	Guangdong	Wang and Bau (2014)
	P. rugocephala	Hong Kong	Wang and Bau (2014)
	P. subincerta	Guangdong	Bi (1991)
	P. tristis	Guangdong	Wang and Bau (2014)

of these species have been described as novel species from China (Bi 1991; Yan and Bau 2017; Yan 2018; Yan et al. 2019; Bau and Yan 2021a, 2021b). In Yunnan Province, a total of nine *Psathyrella* species were recorded, viz. *P. alpina* T. Bau & J.Q. Yan, *P. bipellis* (Quél.) A.H. Sm., *P. campestris* (Earle) A.H. Sm., *P. lactobrunnescens* A.H. Sm., *P. oboensis*, *P. piluliformis*, *P. piluliformoides*, *P. spadiceogrisea* (Schaeff.) Maire, and *P. tintinnabula* J.Q. Yan (Yan 2018; Yan and Bau 2018b; Li et al. 2019; Yan et al. 2019; Bau and Yan 2021b; Liang et al. 2023; Zhang 2024). In this study, *P. qujinguniversitatica* and *P. yunnanensis* are described as new species. Therefore, a total of 55 *Psathyrella* species have been recorded in China. However, the nine species were identified only through morphological classification, which is insufficient for accurately assigning their taxonomic placement and requires molecular data to determine their section placement.

Yunnan Province, with its highly diverse ecological environments, harbors a wide range of organisms, including animals, plants, and fungi (Feng and Yang 2018; Wang et al. 2021; Li et al. 2024). Given this remarkable biodiversity, it is likely that numerous species remain undocumented. Consequently, further systematic surveys are essential to more comprehensively characterize the diversity and distribution of the genus *Psathyrella*. This study provides information on two new *Psathyrella* species, thereby enriching the current mycological research dataset on *Psathyrella* and providing evidence for future taxonomic, phylogenetic, and distributional studies.

Acknowledgments

This research was supported by the National Natural Science Foundation of China (Number 32260004). Samantha C. Karunarathan and Saowaluck Tibpromma thank the High-Level Talent Recruitment Plan of Yunnan Province (High-End Foreign Experts program), the Key Laboratory of Yunnan Provincial Department of Education of the Deep-Time Evolution on Biodiversity from the Origin of the Pearl River, for their support. The authors extend their appreciation to the Ongoing Research Funding Program (ORF-2026-558), King Saud

University, Riyadh, Saudi Arabia. Nakarin Suwannarach and Jaturong Kumla thank Chiang Mai University for the support. Dege Zheng and Meiyan Han thank the CMU Presidential Scholarship (MS) for supporting their M.Sc. studies. The authors thank Dr. Pietro Voto for sharing important references related to this study and Shaun Pennycook for his suggestions on the Latin names.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

Funding

The National Natural Science Foundation of China (Number 32260004) and the Ongoing Research Funding Program (ORF-2026-558), King Saud University, Riyadh, Saudi Arabia.

Author contributions

Conceptualization: SCK, ST, JK, and WHL. Data curation: DGZ, JK, WHL, and LJZ. Formal analysis: SCK, ST, JK, and NS. Funding acquisition: SCK, ST, DDQ, and AME. Investigation: SCK, WHL, and DGZ. Methodology: DGZ, SCK, JK, KC, and EC. Project administration: SCK, ST. Resources: DGZ. Software: DGZ, WHL, MYH, JK, and LJZ. Supervision: SCK, JK, NK, and ST. Validation: SCK, JK, NK, and ST. Visualization: SCK, JK, and DGZ. Writing - original draft: DGZ. Review, and editing: SCK, ST, JK, NS, EC, WHL, AME, DQD, LJZ, and MYH.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

Bau T, Yan JQ (2021a) A new genus and four new species in the/*Psathyrella* sl clade from China. MycoKeys 80: 115–131. https://doi.org/10.3897/mycokeys.80.65123

Bau T, Yan JQ (2021b) Two new rare species of *Candolleomyces* with pale spores from China. MycoKeys 80: 149. https://doi.org/10.3897/mycokeys.80.67166

Bhunjun CS, Niskanen T, Suwannarach N, Wannathes N, Chen YJ, McKenzie EHC, Maharachchikumbura SSN, Buyck B, Zhao CL, Fan YG, Zhang JY, Dissanayake AJ, Marasinghe DS, Jayawardena RS, Kumla J, Padamsee N, Chen YY, Liimatainen K, Ammirati J, Phukhamsakda C, Liu JK, Phonrob W, Randrianjohany E, Hongsanan S, Cheewangkoon R, Bundhun D, Khuna S, Yu WJ, Deng LS, Lu YZ, Hyde KD, Lumyong S (2022) The numbers of fungi: Are the most speciose genera truly diverse? Fungal Diversity 114: 387–462. https://doi.org/10.1007/s13225-022-00501-4

Bi ZS (1991) Two new species of *Psathyrella* and *Gymnopilus* from Guangdong Province. Guihaia 11: 131–134.

Cen J, Gao GP, Wan Y (2021) Species of *Agaricus* fungi resources in Tianzhu Mountain, Shenyang. Journal of Northeast Forestry University 49: 154–158.

Chang GY, Sun C, Wang JR, Bau T (2006) Survey of macrofungi resources in Zuojia Area (Report No. III). Journal of Jilin Agricultural University 28: 505–509.

Desjardin DE, Perry BA (2016) Dark-spored species of agaricineae from Republic of São Tomé and Príncipe, West Africa. Mycosphere 7: 359–391. https://doi.org/10.5943/mycosphere/7/3/8

Feng B, Yang Z (2018) Studies on diversity of higher fungi in Yunnan, southwestern China: A review. Plant Diversity 40: 165–171. https://doi.org/10.1016/j.pld.2018.07.001

Fries EM (1821) Systema mycologicum: sistens fungorum ordines, genera et species, huc usque cognitas, quas ad normam methodi naturalis determinavit. Lundae, Ex Officina Berlingiana, Lund, 520 pp. https://doi.org/10.5962/bhl.title.5378

Fries EM (1838) Epicrisis Systematis Mycologici, seu Synopsis Hymenomycetum. Typographia Academica, Uppsala, 610 pp.

Fries EM (1849) Summa Vegetabilium Scandinaveae. Sectio posterior. Typographia Academica, Stockholm, 259–572.

Gams W (2002) Report of the committee for fungi: 10. Taxon 51: 791–792. https://doi.org/10.2307/1555039

Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes–application to the identification of mycorrhizae and rusts. Molecular Ecology 2: 113–118. https://doi.org/10.1111/j.1365-294X.1993.tb00005.x

Glez-Peña D, Gómez-Blanco D, Reboiro-Jato M, Fdez-Riverola F, Posada D (2010) ALTER: Program-oriented conversion of DNA and protein alignments. Nucleic Acids Research 38: W14–W18. https://doi.org/10.1093/nar/gkq321

Guzmán G, Montoya-Bello L, Bandala-Muñoz VM (1988) A new species of *Psathyrella* (Agaricales, Coprinaceae) from Mexico with discussions on the known species. Brittonia 40: 229–234. https://doi.org/10.2307/2807012

Hall TA (1999) BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41: 95–98.

Hansen L, Knudsen H (1992) Nordic macromycetes 2: Polyporales, Boletales, Agaricales, Russulales. Nordsvamp, Copenhagen, 474 pp.

Hu YW, Karunarathna SC, Li H, Galappaththi MC, Zhao CL, Kakumyan P, Mortimer PE (2022) The impact of drying temperature on basidiospore size. Diversity 14: e239. https://doi.org/10.3390/d14040239

Index Fungorum (2026) Index Fungorum. http://www.indexfungorum.org/Names/Names.asp [accessed 28 January 2026]

Katoh K, Standley DM (2016) A simple method to control over-alignment in the MAFFT multiple sequence alignment program. Bioinformatics 32: 1933–1942. https://doi.org/10.1093/bioinformatics/btw108

Katoh K, Rozewicki J, Yamada K (2019) MAFFT online service: Multiple sequence alignment, interactive sequence choice and visualization. Briefings in Bioinformatics 20: 1160–1166. https://doi.org/10.1093/bib/bbx108

Keirle MR, Hemmes DE, Desjardin DE (2004) Agaricales of the Hawaiian Islands. 8. Agaricaceae: *Coprinus* and *Podaxis*; Psathyrellaceae: *Coprinopsis*, *Coprinellus* and *Parasola.* Fungal Diversity 15: 33–124.

Kirk PM, Cannon PF, Minter DW, Stalpers JA (2008) Ainsworth & Bisby's dictionary of the fungi, 10th edn. CAB International, Wallingford, 771 pp. https://doi.org/10.1079/9780851998268.0000

Kits van Waveren E (1985) The Dutch, French, and British species of *Psathyrella.* Persoonia (Supplement 2): 3–300.

Kits van Waveren E (1987) Additions to our monograph of *Psathyrella*: Thirteen new species, some revised keys, comments on other recently described species, and corrections and additions to our monograph. Persoonia 13: 327–368.

Kornerup A, Wanscher JH (1978) Methuen handbook of colour (3rd edn.). Eyre Methuen, London, 252 pp.

Kuo M (2020) *Psathyrella piluliformis*. http://www.mushroomexpert.com/psathyrella_piluliformis.html

Lange JE (1939) Flora Agaricina Danica, vols 4–5. Recato A/S, Copenhagen, 105 pp.

Larsson E, Örstadius L (2008) Fourteen coprophilous species of *Psathyrella* identified in the Nordic countries using morphology and nuclear rDNA sequence data. Mycological Research 112: 1165–1185. https://doi.org/10.1016/j.mycres.2008.04.003

Li P, Xiao HY, Liu CM (2019) Investigation on the diversity of macrofungi in Dazhongshan of Nanhua county in Yunnan Province. Guizhou Agricultural Sciences 47: 46–54.

Li MQ, Yan XF, Ren YF, Zhou LB, Deng XJ (2023) Diversity of macrofungi in Liupanshan National Nature Reserve, Ningxia. Mycosystema 42: 1889–1905. https://doi.org/10.13346/j.mycosystema.220501

Li Y, Li TH, Yang ZL, Bau T, Dai YC (2024) Overview: Geographical Partition and Distribution of Fungal Resources in China. Atlas of Chinese Macrofungal Resources. Springer, Singapore, 11–47. https://doi.org/10.1007/978-981-99-6315-7_3

Liang XN, Gao YJ, Zhang HY, Zhang Y (2023) Research on macrofungal diversity in Southern sectionportion of Gaoligongshan. Journal of Southwest Forestry University 43: 97–105. https://doi.org/10.11929/j.swfu.202210067

Liu CM, Li P, Yang B (2020) Research on diversity of macrofungi in Xujiaba of Jingdong county in Yunnan Province. Hubei Agricultural Sciences 59: 105–115.

Mao XL (1997) Preliminary report on macrofungi research in Ningxia. Ningxia Agricultural and Forestry Science and Technology 5: 1–6.

Matheny PB, Curtis JM, Hofstetter V, Aime MC, Moncalvo J-M, Ge ZW, Yang ZL, Slot JC, Ammirati JF, Baroni TJ, Bougher NL, Hughes KW, Lodge DJ, Kerrigan RW, Seidl MT, Aanen DK, DeNitis M, Daniele GM, Desjardin DE, Kropp BR, Norvell LN, Parker A, Vellinga EC, Vilgalys R, Hibbett DS (2006) Major clades of Agaricales: A multilocus phylogenetic overview. Mycologia 98: 982–995. https://doi.org/10.1080/15572536.2006.11832627

Miller MA, Pfeiffer W, Schwartz T (2012) The CIPRES Science Gateway: Enabling High-impact Science for Phylogenetics Researchers with Limited Resources. Proceedings of

the 1st Conference of the Extreme Science and Engineering Discovery Environment: Bridging from the Extreme to the campus and beyond. Association for Computing Machinery, New York, 39: 1–8. https://doi.org/10.1145/2335755.2335836

Muñoz G, Musumeci E, Deschuyteneer D, Olariaga I (2022) *Psathyrella griseovelata* sp. nov. (Basidiomycota, Psathyrellaceae), encontrada en La Rioja (España). Fungi Iberici 2: 27–39. https://doi.org/10.51436/funiber/02.002

Nagy LG, Vágvölgyi C, Papp T (2013) Morphological characterization of clades of the Psathyrellaceae (Agaricales) inferred from a multigene phylogeny. Mycological Progress 12: 505–517. https://doi.org/10.1007/s11557-012-0857-3

Natarajan K (1978) South Indian Agaricales IV. A new species of *Psathyrella*. Mycologia 70: 1259–1261. https://doi.org/10.1080/00275514.1978.12020347

Nylander JAA (2004) MrModeltest v2.0. Program distributed by the author, Evolutionary Biology Centre, Uppsala, Sweden.

Örstadius L (2007) Studies on *Psathyrella* within the project Funga Nordica. Agarica : Mykologisk Tidsskrift 27: 64–90.

Örstadius L, Huhtinen S (1996) The psathyrelloid taxa described by P. A. Karsten. Österreichische Zeitschrift für Pilzkunde 5: 131–148.

Örstadius L, Ryberg M, Larsson E (2015) Molecular phylogenetics and taxonomy in Psathyrellaceae (Agaricales) with focus on psathyrelloid species: Introduction of three new genera and 18 new species. Mycological Progress 14: 1–42. https://doi.org/10.1007/s11557-015-1047-x

Padamsee M, Matheny PB, Dentinger BTM, McLaughlin DJ (2008) The mushroom family Psathyrellaceae: Evidence for large-scale polyphyly of the genus *Psathyrella*. Molecular Phylogenetics and Evolution 46: 415–429. https://doi.org/10.1016/j.ympev.2007.11.004

Pegler DN (1977) A preliminary agaric flora of East Africa. Kew bulletin additional series, 6. Her Majesty's Stationery Office, London, 615 pp.

Plasterer TN (1997) Seqman. In: Swindell SR (Ed.) Sequence Data Analysis Guidebook. Springer Press, Berlin, 75–89. https://doi.org/10.1385/0-89603-358-9:75

Quélet L (1872) Les champignons du Jura et des vosges. Mémoires de la Société d'Émulation de Montbéliard 5: 43–332.

Rambaut A, Drummond AJ (2012) FigTree version 1.4. 0. http://tree.bio.ed.ac.uk/software/figtree

Rathnayaka AR, Tennakoon DS, Jones GE, Wanasinghe DN, Bhat DJ, Priyashantha AH, Stephenson SL, Tibpromma S, Karunarathna SC (2024) Significance of precise documentation of hosts and geospatial data of fungal collections, with an emphasis on plant-associated fungi. New Zealand Journal of Botany 63: 462–489. https://doi.org/10.1080/0028825X.2024.2381734

Redhead SA, Vilgalys R, Moncalvo JM, Johnson J, Hopple Jr JS (2001a) *Coprinus* Pers. and the disposition of *Coprinus* species *sensu lato*. Taxon 50: 203–241. https://doi.org/10.2307/1224525

Redhead SA, Vilgalys R, Moncalvo JM, Johnson J, Hopple Jr JS (2001b) Proposals to conserve the name *Psathyrella* (Fr.) Quel. with a conserved type and to reject the name *Pselliophora* P. Karst. (Basidiomycetes: Psathyrellaceae). Taxon 50: 275–278. https://doi.org/10.2307/1224529

Ronquist F, Teslenko M, Van Der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Singer R (1951) Type study on basidiomycete V. Sydowia 5: 445–475.

Singer R (1975) The Agaricales in modern taxonomy (3rd edn.). Verlag Von J. Cramer, Germany, 912 pp. https://doi.org/10.1127/nova.hedwigia/26/1975/435

Smith AH (1972) The North America species of *Psathyrella*. The New York Botanical Garden, America, 633 pp.

Stamatakis A (2006) RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22: 2688–2690. https://doi.org/10.1093/bioinformatics/btl446

Stamatakis A (2014) RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30: 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Stamatakis A, Ludwig T, Meier H (2005) RAxML-III: A fast program for maximum likelihood-based inference of large phylogenetic trees. Bioinformatics 21: 456–463. https://doi.org/10.1093/bioinformatics/bti191

Takahashi H (2000) Two new species and one new variety of Agaricales from central Honshu, Japan. Mycoscience 41: 15–23. https://doi.org/10.1007/BF02464381

Tarafder E, Karunarathna SC, Dutta AK, Elgorban AM, Tian FH, Acharya K (2025) Morphology and phylogeny reveal two new species and a new geographical record of *Agaricus* sect. *Rubricosi* (Agaricales) from West Bengal, India. Scientific Reports 15: 25190. https://doi.org/10.1038/s41598-025-08102-2

Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. Journal of Bacteriology 172: 4238–4246. https://doi.org/10.1128/jb.172.8.4238-4246.1990

Voto P (2011) *Psathyrella carinthiaca* sp. nov. e nuove segnalazioni di *P. bivelata.* Rivista di Micologia 54: 121–133.

Voto P (2020) Novelties in the family Psathyrellaceae. Part IV. Rivista Micologica Romana, Bolletino dell'Associazione Micologica Ecologica Romana 110: 87–91.

Voto P, Setti L, Maraia G, Tacconi A, Milanese V (2020) Some rare or interesting species of fungi. Rivista Micologica Romana, Bolletino dell'Associazione Micologica Ecologica Romana 110: 73–80.

Wächter D, Melzer A (2020) Proposal for a subdivision of the family Psathyrellaceae based on a taxon-rich phylogenetic analysis with iterative multigene guide tree. Mycological Progress 19: 1151–1265. https://doi.org/10.1007/s11557-020-01606-3

Walther G, Garnica S, Weiß M (2005) The systematic relevance of conidiogenesis modes in the gilled Agaricales. Mycological Research 109: 525–544. https://doi.org/10.1017/S0953756205002868

Wang Y, Bau T (2014) Well-known Chinese species of *Psathyrella* and their distribution. Journal of Fungal Research 12: 133–141.

Wang K, Chen SL, Dai YC, Jia ZF, Li TH, Liu TZ, Phurbu D, Mamut R, Sun GY, Bau T, Wei SL, Yang ZL, Yuan HS, Zhang XG, Cai L (2021) Overview of China's nomenclature novelties of fungi in the new century (2000–2020). Mycosystema 40: 822–833. https://doi.org/10.13346/j.mycosystema.210064

Wang K, Du Z, Guo YB, Liu TZ, Xie ML, Zhao MJ, Liu DM, Li GJ, Wei TZ (2024) Diversity of macrofungi in Taihang Mountains of Beijing and Hebei, North China. Mycosystema 43: 142–177. https://doi.org/10.13346/j.mycosystema.230311

Wei YZ (2017) Survey of large wood-decaying fungi resources in the water conservation forest of the Hunhe River in Wandianzi. Protection Forest Science and Technology 10: 40–45.

White TJ, Bruns T, Lee S, Taylor JW (1990) Amplification and Direct Sequencing of Fungal Ribosomal RNA Genes for Phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ,

White TJ (Eds) PCR Protocols: A guide to Methods and Applications. San Diego, CA: Academic Press, New York, 315–322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Yan JQ (2018) Taxonomy and molecular phylogeny of *Psathyrella* and related genera in China. PhD Thesis, Jilin Agricultural University, Jilin, China.

Yan JQ, Bau T (2017) New and newly recorded species of *Psathyrella* (Psathyrellaceae, Agaricales) from Northeast China. Phytotaxa 321: 139–150. https://doi.org/10.11646/phytotaxa.321.1.7

Yan JQ, Bau T (2018a) The Northeast Chinese species of *Psathyrella* (Agaricales, Psathyrellaceae). MycoKeys 33: 85–102. https://doi.org/10.3897/mycokeys.33.24704

Yan JQ, Bau T (2018b) *Psathyrella alpina* sp. nov. (Psathyrellaceae, Agaricales), a new species from China. Phytotaxa 349: 85–91. https://doi.org/10.11646/phytotaxa.349.1.11

Yan JQ, Bau T (2021) A new and two newly recorded species in the */pygmaea* clade of *Psathyrella* (Psathyrellaceae, Agaricomycetes) from China. Mycosystema 40: 462–472. https://doi.org/10.13346/j.mycosystema.200350

Yan JQ, Ge YP, Hu DM, Zhou JP, Huo GH (2019) *Psathyrella tintinnabula* sp. nov. (Psathyrellaceae, Agaricales), a new species from southwest China. Phytotaxa 400: 64–70. https://doi.org/10.11646/phytotaxa.400.2.2

Ying JZ (1994) Large economic fungi in Southwest China. Science Press, Beijing, 399pp.

Zhang JM (2024) Studies on Macrofungi Diversity in Xinglong Mountain National Nature Reserve. Master Thesis, Northwest Normal University, Ningxia Hui Autonomous Region, China.

Zheng WK (1988) Illustrated Guide to Edible and Poisonous Fungi in Yunnan. Yunnan Science and Technology Press, Kunming, 175 pp.

Zheng DG, Voto P, Tibpromma S, Lu WH, Han MY, Kumla J, Suwannarach N, Dai DQ, Zhang LJ, Elgorban AM, Chukeatirote E, Karunarathna SC (2025) *Candolleomyces yunnanensis* (Psathyrellaceae, Agaricales), a novel species from Yunnan Province, China. Phytotaxa 711: 281–292. https://doi.org/10.11646/phytotaxa.711.3.3

Supplementary material 1

Supplementary information

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